The mechanical handling of food by the alimentary canal of Orthoptera and allies

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(Láms. VI-VII)

Dufour's classic "Recherches Anatomiques et Physiologiques sur les Orthoptères" (1841) contained an early comparative treatment of the digestive canal in Orthoptera and allies. Since Dufour many workers have contributed studies relating to the alimentary system of these important, interesting insects. Among the more salient are those of Bordas (various papers, especially 1897, 1897 a), dealing with the morphology of the digestive tracts of various orthopteroids, and Walker (1949), summarizing present-day knowledge on the subject. More specialized contributions have been made by Albrecht (1953, 1956), Bryantseva (1951), Carpentier (1937), Hodge (1936, 1939, 1940, 1943), Williams (1954), and many others. In none of the published work has there been detailed discussion of possible relationships between the structure of the tract and the nature of the food mass it handles mechanically.

Orthopterists now have at their disposal a general understanding of food-habits in selected species. Once information of this type becomes available, it is a matter of time before adaptive modifications for feeding come under scrutiny. Isely (1944) pioneered in this direction. He showed that the mandibles of grasshoppers and katydids are adapted in form and armature to the foods they handle. More recently, Chapman (1964) and the author (Gangwere, 1960, 1961, 1965) have been concerned with mouthpart adaptation. It is now apparent that a close correlation exists between the mouthparts of Orthoptera and allies, the insects' food, and their feeding pattern.

We are led to ask whether the digestive tract, like the mouthparts, exhibits correlations between its gross structure and the foods it handles. It is in answer to this question that the present investigation was initiated. It involved two general activities: (1) studies on gross features of the alimentary canal, and (2) studies on the foods it handles mechanically and physiologically. In carrying out the first, the author examined specimens of sixteen species of alcohol-preserved orthopteroids to detect possible adaptive modifications. The gross structure of the gut was studied under a binocular dissecting microscope, and then the denticles and other finer features were examined under the higher power of a compound microscope. The species were selected on the basis of distribution in taxonomic groups (every major family in Michigan had representation) and of food-habits typical of the groups they represent. The following species and groups were included:

BLATTOIDEA (Cockroaches)
Parcoblatta uhleriana (Saussure)

MANTOIDEA (Praying Mantids)
Tenodera aridifolia sinensis Saussure

PHASMOIDEA (Walking-Sticks and Allies)
Diapheromera femorata (Say)

ACRIDOIDEA: TRUXALINE (Slant-Faced Grasshoppers)
Syrbula admirabilis (Uhler)

ACRIDOIDEA: CANTANTOPINAE (Spine-Breasted Grasshoppers)
Melanoplus f.-r.(femur-rubrum (DeGeer), *M. keeleri luridus* Dodge, *M. s. sanguinipes* (Fabricius), *Schistocerca lineata* Scudder

TETTIGONOIDEA: PHANEROPTERINAE (Bush and Round-Headed Katydids)
Amblycorypha oblongifolia (DeGeer), *A. rotundifolia* (Scudder), *Scudderia c. curvicauda* (DeGeer), *S. f. furcata* Brunner

TETTIGONOIDEA: CONOCEPHALINAE (Meadow Katydids)
Orchelimum gladiator (Bruner)

TETTIGONOIDEA: COPIPHORINAE (Cone-Headed Katydids)
Neoconocephalus ensiger (Harris)

GRYLLOIDEA: GRYLLINAE (Field Crickets)
Gryllus pennsylvanicus (Burmeister)

GRYLLOIDEA: OECANTHINAE (White Tree Crickets)
Oecanthus quadripunctatus Beutenmuller

Following completion of the gross study, the texture and configuration of food morsels was investigated as follows: (a) individuals of forty-three species were watched one or more times, each, as they fed, making possible an evaluation of characteristic damage inflicted on food; (b) remnants of plants subjected to feeding by Orthoptera were preserved in F. A. A. solution and later analyzed for damage; and (c) food fragments recovered from the crops of fifty-eight species were examined to determine morsel size, shape, and alignment (if any). The food studies were necessary because the nature of the individual food particles ingested determines the structure and consistency of the food mass within the gut.

STRUCTURE OF THE DIGESTIVE TRACT.

The following morphologic section is basic to an understanding of possible adaptive modifications. It is largely abstracted from Bordas (1897, 1897 a), Beier (1933-1934), Carpentier (1937), Snodgrass (1935), Uvarov (1928), Walker (1949), and others but also includes data from the present study.

Four major categories of digestive tract may be recognized among the Orthoptera and allies investigated during this study:

1. *Canal Linear and Without Caeca.* This type is represented by the gut of the Phasmoidea. In the phasmoids (Lám. VI: 1) the salivary glands are well developed and provided with reservoirs; the digestive tract almost perfectly straight, in conformity with the linear body form; the crop cylindrical and scarcely delineated from the tubular, weakly armed proventriculus; the ventriculus subdivided into anterior and posterior regions; the six rectal pads arranged in a single circle; and the numerous Malpighian vessels open into a number of ampullae.

2. *Canal Curved or Convoluted and Ventriculus With Eight Tubular Caeca.* The Blattoidea (Lám. VI: 2) and Mantoidea share many morphologic characteristics and are closely related, a relationship born out by the essential similarity of their digestive tracts. Both have

well developed salivary glands with reservoirs; a large conical or fusiform crop; a conical proventriculus with a unique armature; and a curved or coiled ventriculus and anterior intestine. There are minor differences. In cockroaches the gut is strongly curved or coiled, the proventricular armature powerful, and the numerous Malpighian tubules grouped into six fascicles; in mantids the gut is less curved or (in the more elongate-bodied species) even straight, the proventricular armature rather weakly developed, and the Malpighian tubules not grouped into fascicles.

3. *Canal Curved or Convoluted and Ventriculus With Two Sacculiform Caeca.* The Tettigonoidea (Lám. VI: 3) and Grylloidea have well developed salivary glands with reservoirs; a digestive canal distinctly longer than the body; a voluminous pyriform or strongly asymmetrical crop; a subspherical proventriculus with an anterior neck and a distinctive, usually strongly developed armature; a bent or coiled ventriculus often divided into anterior and posterior segments; sac-like, internally partitioned caeca almost always two in number and morphologically dorsal and ventral in position; and usually an undivided anterior intestine. The two groups differ chiefly with respect to the Malpighian tubules. In the Tettigonoidea these vessels tend to be grouped into six or fewer fascicles discharging into the same number of ampullee; in the Grylloidea there is a single fascicle and ampulla with a duct, the "ureter".

4. *Canal Semilinear and Ventriculus Usually With Six Conical Caeca.* The Acridoidea have a simple digestive tract (Lám. VI: 4) that is actually highly specialized. The salivary glands are diffuse, feebly developed, and without reservoirs; the tract proper is semilinear and subequal to the body; the esophagus short; the crop and the lightly armed proventriculus together form a cylindrical or slightly tapering segment with scarcely a trace of the usual contriction between the two; the proventricular-ventricular valve is either present or is reduced to a slight protrusion of the proventriculus into the ventriculus, forming a groove in which originates the peritrophic membrane; the ventriculus is straight and undivided; its conical caeca normally six in number; each caecum has a caudally directed diverticulum (except in a few species in which they are vestigial); the pyloric valve consists of a transverse fold and sometimes six variably developed, rounded elevations; the anterior intestine is usually divided into two segments, the caudal one of which (the colon) is usually sinuate; and the Malpighian tubules

are grouped into fascicles often discharging into six ampullae (sometimes into five to twelve or more).

Results from the present investigation suggest that the Blattoidea, Grylloidea, Mantoidea, and Tettigonoidea may profitably be considered together in opposition to the Acridoidea and Phasmoidea. The former show many resemblances. In them the crop is a thin-walled, highly distensible sac; the proventriculus a short, muscular, bulbiform or conical organ with an internal armature of sclerotized "teeth" or sometimes soft, setose papillae; and the ventriculus and anterior intestine usually coiled or curved. This type of gut is best characterized by its separation into organs ("segments") of different caliber. The food-habits and mouthparts of the orthopteroids with the "segmented" gut are varied but never of the graminivorous (grass feeding) type (Gangwere, 1961).

In contrast, the Acridoidea (many of which are graminivorous) and the Phasmoidea have a linear or essentially linear gut subequal to the body; the crop is tubular or somewhat fusiform and scarcely delineated from the lightly armed proventriculus; and the ventriculus and anterior intestine are linear (except in many acridoids, in which the colon is lightly sinuate).

PHYSIOLOGY OF THE DIGESTIVE TRACT.

The following section is abstracted from Day and Waterhouse (1953), Uvarov (1948), Wigglesworth (1950), and many other sources noted in the text. Certain conclusions drawn are those of the present author.

Little need be said about the buccal cavity, pharynx, and esophagus, for they are essentially similar throughout the Orthoptera and allies. The pharynx has elaborate dilator muscles that function in ingestion of food previously mixed with saliva. Saliva contains both enzymes and mucoid substances. It apparently functions both in digestion and lubrication. Day and Powning (1949) showed that relatively larger amounts of saliva are swallowed with a dry than with a moist diet. This result suggests that the lubricatory function may be a more important one of insect saliva than has been suspected heretofore. The esophagus seems purely conductive. Sanford (1918) cited the thickness

of the cockroach esophageal intima as evidence that secretion and absorption cannot occur here.

The "Segmented" Digestive Tract. The crop in the Blattoidea, Mantoidea, Grylloidea, and Tettigonoidea acts as a storage organ for large quantities of ingested food. Sometimes it fills the thorax and extends well into the abdomen. Sanford (1918) found that cockroaches fed to repletion on oil and sugar can live for nearly two months on the food supply stored here. In the Blattoidea and perhaps also in the other groups the crop is the site of partial digestion (Wigglesworth, 1950, Day and Waterhouse, 1953) under control both of swallowed salivary enzymes and of enzymes regurgitated from the ventriculus (Abbott, 1926, Day and Powning, 1949, Ramme, 1913). A further function of the crop may be that of fat absorption. Abbott *(l. c.),* Eisner (1955), Sanford *(l. c.),* and Scharrer (1947) showed that fat droplets may be absorbed by crop epithelial cells. More recent work (Treherne, 1958) denies significant absorption of the triglyceride tripalmitin, and casts doubt on this conclusion. Whatever the situation with respect to fats, it seems safe to say that the crop wall is impermeable to other substances (Abbott, *l. c.,* Eidmann, 1922).

The functions of the proventriculus are controversial, but in the Blattoidea, Grylloidea, Mantoidea, and Tettigonoidea it may combine in varying proportions the functions of a valve, a triturating apparatus, and a propulsory organ. In those forms with a powerful proventricular musculature and heavy armature there is little doubt that soft food is shredded and triturated during passage through it. Evidence to this effect was presented by Davis (1927), who noted that wax "pencils" inserted into the proventriculus of living *Stenopelmatus* were indented by the armature; Eidmann (1924), who showed that the strong "teeth" in the anterior part of the proventriculus of *Blatta orientalis* break large pieces of food into smaller ones; and Judd (1948), who found that the great differences in form and strength of the "teeth" in some species indicate corresponding differences in efficacy of trituration. Eidmann's observations *(l. c.)* also indicate that triturated pieces are restrained by the posterior part of the proventriculus until subjected to partial digestion by regurgitated enzymes. This suggests that the proventriculus has a valvular function. DuPorte, too, concluded (1918) that the proventriculus enjoys a multiple function. He maintained that it has both a triturating and a propulsive role. The general remarks about proventricular function cannot hold completely for the Phaneropterinae

and many Rhaphidophorinae, whose "teeth" are represented by soft, setose lobes.

A general characteristic of orthopteroids are folds (sometimes supported by chitinized plates) projecting caudad from the proventriculus into the ventriculus. They compose the proventricular-ventricular valve. This structure inhibits regurgitation from the ventriculus and also ensures that the food mass is enclosed by the peritrophic membrane (Wigglesworth, 1950).

A chitinous peritrophic membrane freely permeable both to digestive enzymes and to the products of digestion is present in nearly all orthopteroids. It is a thin, often laminate membrane that encloses food in the midgut. It serves to keep coarse food particles from contact with the delicate walls of the ventriculus. Its mode of formation is controversial and may not be uniform among the orthopteroids (Berretta, 1937, Day and Waterhouse, 1953, Waterhouse, 1957). In some orthopteroids the peritrophic membrane is destroyed in the anterior intestine, but in Acrididae it is said to remain intact and to surround egested feculae.

The ventriculus and caeca secrete digestive enzymes (including amylases, lipases, and proteases) and absorb digested food. There is a large literature (much of it recent) on this subject. No further details will be given here. It is beyond the scope of this report.

The food mass is withheld within the ventriculus, according to Wigglesworth (1950), by the so-called pyloric valve. In the Blattoidea, Grylloidea, Mantoidea, and Tettigonoidea this valve is well developed. It opens from time to time to admit a quantity of food to the anterior intestine. The latter is a region where much absorption of water takes place. As a result, the intestinal contents become progressively reduced and drier as they move caudad. The rectum (particularly the "rectal pads") has also been regarded by some authorities (Phillips, 1964, Wigglesworth, 1933) as a site of water absorption, but others (Snodgrass, 1935) have maintained that the rectal structure is not indicative of this function.

Food is driven through the alimentary canal as a result of active propulsive contractions of the gut wall. It moves through the intestinal organs in an apparently intermittent fashion, subject to wide variation. The literature includes some data on egestion time. The cockroaches *Periplaneta americana* (Snipes and Tauber, 1937), *P. australasiae* (Abbott, 1926), and *Blattella germanica* (Day and Powning, 1949) require 20.6 hours, 7 hours, and 3 hours, respectively, for passage,

with the food remaining much of the time in the hindgut. This time is increased by starvation (Snipes and Tauber, *l. c.*) and varies with the food (Snipes, 1938). The cricket *Acheta domesticus* requires but 3½ hours for passage (Chauvin, 1946), while the katydid *Tettigonia* needs 32½ hours for passage at a temperature of 18 degrees C., and only 14½ hours at 26 degrees C. (Nielsen, 1943). The latter suggests that temperature, as well as starvation, controls the rate of food passage.

The "Linear" Digestive Tract. Passage of the food mass within the acridoid gut is evidently both fast and continuous, brought about by peristaltic contraction, sometimes aided by folds and caudally directed denticles. Egestion time is rapid in *Locusta* (about 1 hours at 32 degrees C.) (Nenjukov and Parfentjev, 1929) and reasonably so in *Calliptamus* (2 to 3 hours) (Tareeva and Nenjukov, 1931). Environmental factors may retard or accelerate this food passage. Starvation is one such factor. Monchadsky and Skoblo (in Uvarov, 1948) noted that the egestion time of starved *Schistocerca* is 3 to 4 days or more rather than the usual 1½ hours. Food may be another. Tareeva and Nenjukov (1931) found that wheat, a grass, requires 2 hours and 50 minutes to pass through the gut of *Calliptamus,* in contrast to *Polygonum,* a forb, which needs only 2 hours and 15 minutes at the same temperature (28 degrees C.). Temperature is one of the most important factors. Its influence may possibly account for certain discrepancies in the literature. A case in point is *Schistocerca.* Egestion time in this insect was said by one authority (Chauvin, 1946) to be 4 hours and by others (Monchadsky and Skoblo, *l. c.*) to be only 1½ hours.

On the basis of our present incomplete knowledge we can conclude that the physiological action of the various organs of the "linear" digestive tract is not greatly dissimilar from that observed in organs of the "segmented" tract discussed earlier. It is sufficient to note that differences exist, but most appear minor. We need say no more, for such is not the object of this report. Instead, let us turn to the arrangements for handling food mechanically.

CORRELATIONS BETWEEN FOOD-HABITS AND STRUCTURE OF THE ALIMENTARY CANAL.

Given general information on the structure and function of the digestive system in Orthoptera and allies, we can examine the data of

the present study in light of the author's earlier work (1960, 1961) and thereby obtain insight into possible correlations between food-habits and gut structure.

The Orthoptera and allies can be divided into two great, unequal groups on the basis of (1) the texture, consistency, and degree of alignment of the food mass within the alimentary canal and (2) the way in which that system handles food mechanically. One group includes the Acridoidea and Phasmoidea, both with the "linear" gut, and the second the remainder of the orthopteroids, those with the "segmented" gut.

The "Linear" Tract. Grass, taken by "margin feeding", may form an appreciable part or even the entire diet of many grasshoppers. When they eat grass and (to a lesser extent) forb leaves, they cut loose and swallow individual elongate strips (Lám. VII: 5,6). Within the crop the grass morsels become compacted parallel to one another and lie in oblique alignment with respect to the long axis of the alimentary canal. This orientation is maintained as the food column passes largely unbroken through the remainder of the digestive canal to the anus. The tendency is most pronounced in grass feeding truxalines. It is often found that, in dissecting a truxaline, the entire food mass (consisting of parallel grass strips obliquely aligned) can be removed intact from the opened tract.

The internal esophageal surface in grasshoppers is provided with longitudinal ridges and comparatively few denticles, always directed caudad. The danger of mechanical obstruction prohibits transverse ridging and cephalically directed denticles where the lumen is so narrowed. The crop bears numerous, usually transverse rows of denticles figured earlier by Albrecht (1953, 1956), Bryantseva (1951), Tietz (1923), Williams (1954), and others. These denticles are effective in restraining food, especially when the individual morsels are strips longer than the diameter of the proventriculus. This mechanism of the crop makes unnecessary on the part of the proventriculus any well developed restraining valve or armature. The proventriculus is, therefore, free to take on a cylindrical, comparatively unarmed, and longitudinally ridged structure. Such form is not only practical but necessary. An armed proventriculus would be selected against in grasshoppers because of the likelihood of obstruction. Caudad of the proventriculus the digestive tract is linear or almost so (except for the sinuate colon); only an uncon-

voluted canal can accommodate elongate food particles. Any ridging caudal of the crop is necessarily longitudinal (Lám. VI : 4).

In acridids the salivary glands are reduced, so salivary enzymes cannot play much part in digestion. In view of the rapid rate at which the food mass progresses, it is presumed that enzymatic action must be both rapid and effective and absorption equally so. The six large ventricular caeca and diverticula greatly increase the secretory surface and discharge their products uniformly around the periphery of the food colum. Nevertheless, passage is so rapid that the resulting feculae are invariably composed of scarcely digested vegetable remains that retain much of their original structure. The digestive tract tapers to a smaller diameter toward the posterior section of the anterior intestine (the colon). This indicates that compression and water absorption occur here. The colon, according to Goodhue (1963), constricts and separates a short length of food from the semicontinuous food column. The peritrophic membrane surrounding it is then broken as the colon assumes its characteristic S-shape. The resulting fecal pellet is extruded through the anus. Any alignment of food strips observable in the food column is still evident in the feculae (Lám. VII : 7).

The preceding explains the peculiar aligned feculae characteristic of graminivorous (grass feeding) grasshoppers. The slender food morsels ingested are sometimes longer than the diameter of the gut. They cannot assume a position other than a linear or obliquely aligned one as they pass rapidly along the length of the unconstricted, poorly valved, semilinear digestive tract. They maintain this alignment even as they are expelled as feculae through the anus.

Though all acridoids have this type of digestive system, most species are not wholly graminivorous and many are not graminivorous at all. The most strongly graminivorous are the Acridinae and Truxalinae, slant-faced, slender grasshoppers in which the canal is strongly linear. *Radinotatum* (Hodge, 1940) and *Syrbula* (Lám. VI : 4) illustrate this type. The related *Stenobothrus* (Dufour, 1841) and certain other genera may have a slightil sinuous tract. Most Cantantopinae and Cyrtacanthacridinae are forbivorous (broad-leaved herb feeding), dendrophagous (woody plant foliage feeding), or forbivorous-graminivorous. Almost invariably they exhibit more evident valvular constrictions, variations in diameter and proventricular armature, and a somewhat S-shaped anterior intestine. *Nomadacris* (Albrecht, 1956) illustrates this type. The tracts of the related but strongly graminivorous *Leptysma* and

Opshomala (Hodge, 1943) prove an exception. They provide a clear example of convergence toward the type of the acridines and truxalines.

The Phasmoidea resemble the Acridoidea in their "margin feeding," their straight, unsegmented alimentary canal, and their weak proventricular armature (Lám. VI: 1). Notwithstanding these similarities they are, at best, only remotely related to the Acridoidea. They are dendrophagous (woody plant foliage feeding). The individual morsels they ingest are strikingly square (not elongate), and within their intestine there is no alignment of food particles comparable to that seen in Acrididae. The internal surface of their crop and proventriculus bears longitudinal ridges set with denticles. Their linear digestive tract appears to be a consequence of possession of an elongate body form. It is not derived from adaptation to graminivory.

The "Segmented" Tract. The second group of Orthoptera on the basis of the texture and consistency of the food mass and the way in which it is mechanically handled by the gut includes the great majority of species and groups. Numbered among them are the Blattoidea, Mantoidea, Grylloidea, and Tettigonoidea. They are various in their food-habits. They are alike in that they ingest small, irregular pieces or soft, semifluid materials and pulp requiring no particular orientation within the gut (Lám. VII: 9, 10). Such morsels are capable of passage through restricted openings. In these orthopteroids the salivary glands are well developed; the crop a prominent, distensible organ in which food may remain for comparatively long periods of time and be partly digested; the proventriculus strongly valved and often adapted for triturating and restraining larger food fragments until they have been reduced to the proper fineness; the ventriculus and anterior intestine elongate and bent or coiled; and the pyloric and rectal valves usually well developed (Lám. VI: 3). Such a "segmented" digestive tract is adapted for handling food in steps. The food mass is retained in each segment of the canal until a given stage in the digestive process has been reached and is then passed on to the next caudal segment. Food transit, therefore, is intermittent and the time required comparatively long and variable.

The digestive tract of many Tettigonoidea is typical. The esophagus is provided with longitudinal ridges and comparatively few caudally directed denticles. The crop, a highly distensible sac for storage, is lightly muscularized and has few denticles. It contrasts with the grasshopper crop (a heavily muscularized one armed with numerous denticles

arranged in somewhat transverse rows). The food consists of compara-
tively fine, irregular fragments and pulp. Because the crop lacks den-
ticles to retard passage and the food tends to be fine, the proventriculus
is necessarily constricted, highly muscularized, and armed with sizable
denticles.

The preceding explains the unaligned feculae of katydids. The
morsels they ingest take on no particular orientation within the gut:
hence, the lack of alignment that characterizes the food column through-
out the length of the intestine inevitably results in unaligned feculae
(Lám. VII: 8).

Orthopteroids with the "segmented" digestive canal include "center
feeding" omnivores, forbivores (broad-leaved herb feeders), seminivores
(grass "seed" feeders), carnivores, and dendrophages (woody plant fo-
liage feeders). None eats grass foliage to any great extent, and the
few that do take grass ingest non-elongate morsels. The phytophagous
representatives take their food plants in the form of irregular fragments,
pulp, pollen, and fluids. The carnivores and omnivores eat a mostly
semifluid or pulpy food. This may account for the fact that mantids
(which are exclusively carnivorous) and many rhaphidophorines (which
are either carnivorous or omnivorous-carnivorous) have reduced pro-
ventricular armature; in them the proventriculus seems to function
largely as a valve.

It is often said that herbivores have long digestive tracts in com-
parison with those of carnivores. This well-known generalization has
been applied with some success to vertebrates and has been discussed
in connection with insects (Anadon, 1949, Werner, 1894, and others).
This relationship does not hold for the Orthoptera and allies. It is
true that the exclusively carnivorous mantids generally have a shorter,
straighter gut than their omnivorous relatives, the cockroaches. Ne-
vertheless, the Decticinae, Listroscelinae, Saginae, and other katydids
with strongly developed predatory habits have convoluted digestive
tracts no shorter than those of their purely phytophagous relatives.
With respect to the strictly phytophagous orthopteroids, the gut may
be short (as in the Acridoidea and Phasmoidea) or long and coiled (as
in the Phaneropterinae and many other katydid groups). The linear
tract of certain mantids is probably a consequence of their elongate body
form, which often approaches that of phasmids. We can conclude that
caeca, internal ridging, and length must each be taken into consideration

if we hope to obtain a realistic measurement of absorptive and secretive surface.   Length alone is not an accurate index.

Summary and Conclusions.

On the basis of structure and function, four major kinds of digestive tract may be recognized among the groups of Orthoptera and allies investigated during this study: the phasmoid, blattoid-mantoid, tettigonoid-grylloid, and acridoid types.   These may be further aggregated into two great unequal categories based on the insects' method of handling food mechanically within the canal.   The first group includes the "margin feeding" Acridoidea and Phasmoidea, insects with an essentially "linear" gut.

Acridoids ingest elongate strips of grass or sometimes forb foliage. These strips become compacted roughly parallel to one another and lie in oblique alignment with respect to the crop.   They maintain this orientation as they move through the remaining portions of the tract. Such a gut is relatively linear; its proventriculus lightly armed and reduced; its valves and constrictions greatly reduced.   Each of these adaptations contributes to a food passageway of relatively uniform diameter, in which movement of food by peristalsis and pressure from caudally directed denticles is rapid and continuous.   This type of tract is an adaptation for a graminivorous diet.   It is best developed in acridines and truxalines (which are almost exclusively graminivorous) and less well developed in cantantopines, cyrtacanthacridines, and other forbivorous, dendrophagous, or forbivorous-graminivorous Acridoidea.   Significantly, *Leptysma* and certain graminivorous acridoids belonging to predominately forbivorous subfamilies have a digestive tract approaching that of acridines and truxalines.   This is a result of convergence. The food habit exerts, in this case, stronger evolutionary influence than does phylogeny.

The linear gut of the Phasmoidea presents a situation radically different from that of acridoids.   The straight intestine of walking-sticks and allies apparently results from a linear body form.

The second great group of Orthoptera and allies on the basis of method of handling food mechanically within the gut includes the "center feeding" Blattoidea, Mantoidea, Grylloidea, and Tettigonoidea. These insects, characterized by a "segmented" gut, ingest comparati-

ve¹y fine, irregular pieces, pulp, or semifluid food substances capable
of passing through restricted openings and requiring no particular
orientation within the gut. The food mass is first stored in the highly
distensible crop in which it may be partly digested before being passed
on to the next segment, the proventriculus. The latter, a muscular
and usually strongly armed organ, may triturate and restrain larger
food fragments. The food is then released to the remainder of the di-
gestive canal. Caudad of the crop the gut is relatively long and bent
or coiled and its valves well developed. Such a tract is adapted for
handling food in steps, and the food mass is retained in each segment
until given stages in the digestive process have been reached. Among
the orthopteroids with this type of digestive canal are forbivores, omni-
vores, seminivores, carnivores, and dendrophages. None eats grass
to any great extent. Certain of the carnivores are characterized by a
partial loss of proventricular armature, presumably made possible by
a semifluid diet.

The generalization that herbivores have longer intestines than do
carnivores does not hold in the Orthoptera and allies.

It appears there is a positive correlation between the type of diges-
tive canal developed in Orthoptera and allies, the kind of food eaten, and
the method with which the latter is handled mechanically within the gut.

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EXPLANATION OF LAM. VI

Fig. 1.—Linear alimentary canal of the walking-stick *Diapheromera femorata* (Phasmoidea), showing lack of caeca.

Fig. 2.—"Segmented", coiled alimentary canal of the cockroach *Parcoblatta pensylvanica* (Blattoidea), showing six of the eigth caeca.

Fig. 3.—"Segmented", coiled alimentary canal of the katydid *Amblycorypha rotundifolia* (Tettigonoidea: Phaneropterinae), showing the two caeca.

Fig. 4.—Linear alimentary canal of the grasshopper *Syrbula admirabilis* (Acridoidea: Truxalinae), showing four of the six caeca and their caudal diverticula.

ca- Caecum	*o*- Oesophagus
cr- Crp	*pr*-Proventriculus ("gizzard")
di- Diverticulm	*r*- Rectum
int-Anterior intestine	*rp*-Rectal "pad"
mt-Malpighian tubules	*vt*-Ventriculus ("stomach")

EXPLANATION OF LAM. VII

Fig. 5.—Angulate incision taken from grass leaf by "margin feeding" in the grasshopper *Syrbula admirabilis* (Acridoidea: Truxalinae).

Fig. 6.—Individual grass morsels, or "bites", eaten by the grasshopper *Pseudopomala brachyptera* (Acridoidea: Truxalinae). Numerous slender, flat morsels of this type become compacted parallel to one another within the digestive tract. The food column they form maintains its "aligned" particle orientation throughout the length of the gut and even when broken into segments and extruded through the anus as feculae.

Fig. 7.—"Aligned" fecula of the grasshopper *Syrbula admirabilis*. A fecal pellet of this type is composed of numerous slender grass morsels compacted parallel to one another. It exhibits exactly the same particle orientation as does the food column from which it was compressed and "pinched off".
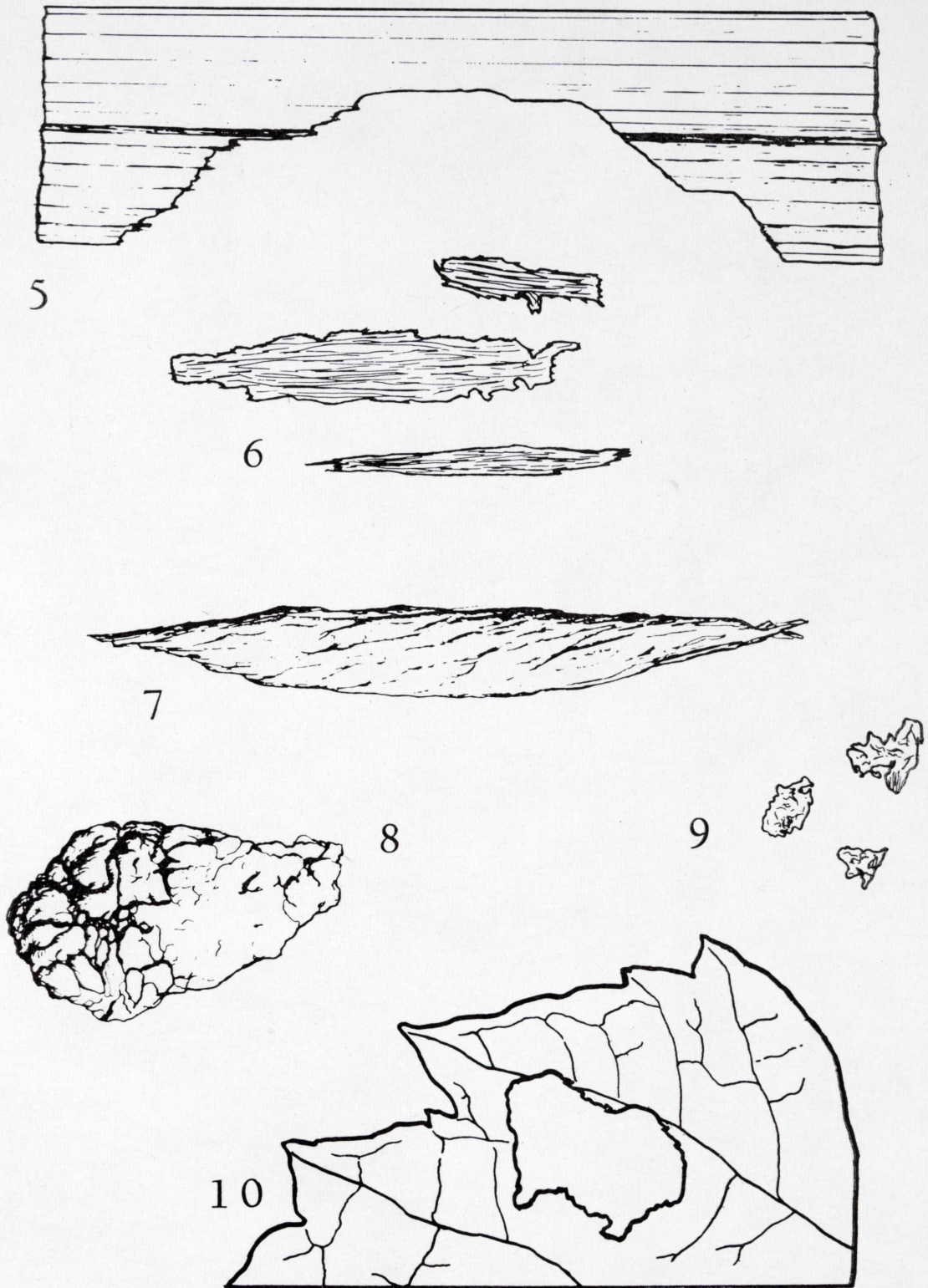
Fig. 8.—"Unaligned" fecula of the katydid *Scudderia c. curvicauda* (Tettigonoidea: Phaneropterinae). A fecal pellet of this type is composed of fine, irregular morsels incised from forbs (broad-leaved herbs) or leaves of woody plants. It exhibits the same lack of fixed particle orientation ar does the column from which it was "pinched off".

Fig. 9.—Individual forb morsels, or "bites", eaten by the katydid *Scudderia c. curvicauda*. Numerous morsels of this type compose the food colum within the intestine. They are comparatively fine and irregular, so take on no particular orientation within the gut.

Fig. 10.—Irregular incision taken from forb leaf by "center feeding" in the katydid *Amblycorypha oblongifolia* (Tettigonoidea: Phaneropterinae).
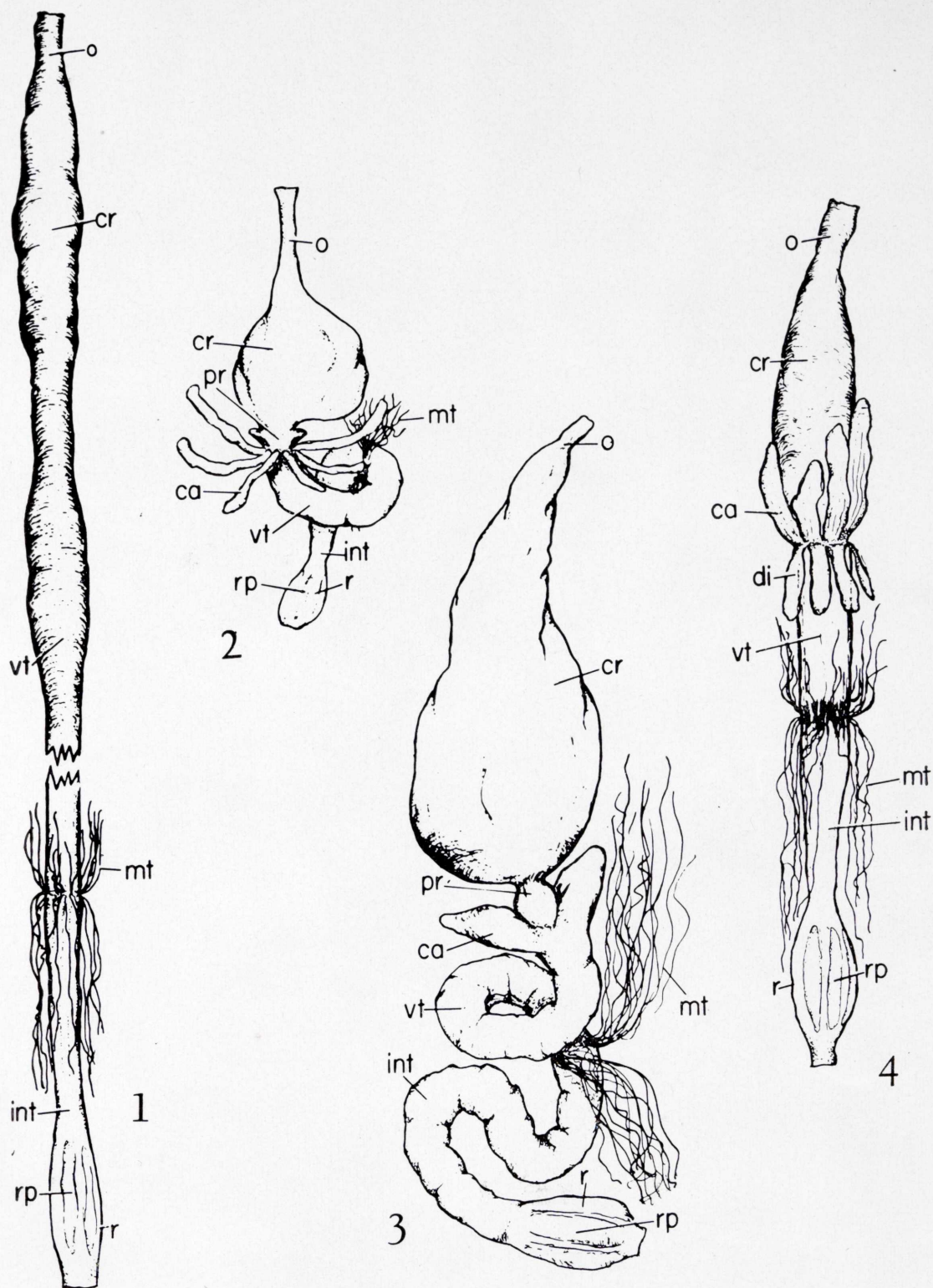
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